ANT DISTRIBUTION IN A SOUTHERN ENGLISH HEATH

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The density distribution of ants in lowland heath formed on Bagshot sands and clays in the Poole basin is being studied; here, a preliminary survey is described.

Diver & Good (1934) planned a comprehensive faunistic survey of a similar though more coastal area and so far the plants (Good 1935), the orthoptera (Diver & Diver 1933), the birds (Lack & Venables 1937), and parts of some other groups (mentioned in Diver 1938 and 1940) have been reported. In addition Good (1948) has produced a detailed account of the geology, topography, climate, soil and flora of Dorset which includes these heaths. They have also been fully discussed by Tansley (1939).

An area of about 8 ha at the west end of Hartland National Nature Reserve was selected for special study (this is 2 miles south-east of Wareham with National Grid reference at centre SY 942852). It provides a good range of variation in height (2–30 m above sea level), in soil moisture (from bog to dry soil on rock) in aspect (it has a central almost conical knoll) and in soil (predominantly sandy but with patches of clay and gravel). The vegetation varies as a consequence and though mostly dominated by *Calluna vulgaris* (L.) Hull, and frequently swept by fire it contains small areas of tree regeneration (mainly *Betula pendula* Roth. and *Pinus sylvestris* L.). Light grazing by the rabbit (*Oryctolagus cuniculus* (L.)) is regular but by no larger mammal.

The area has a long history of human interference. It has probably been open heathland with scrub since at least the twelfth century and there is evidence that ironstone was mined before that. Many trackways both mediaeval and more recent (connected perhaps with the transport of clay to Poole Harbour) have left rough corrugations. In one area of wet heath peat has been cut. About 1880 *Pinus sylvestris* was planted but cut after a fire in 1916 and not replanted. Since then, the heath has been subject to frequent sporadic fires.

The plantation phase which endured 36 years could have eliminated any pre-existing fauna except in exposed places, like rides and the tops of knolls with shallow soil or in wet areas, for typical woodland ants like *Formica rufa* Linnaeus and *Myrmica ruginodis* Nylander tend to be excluded by pine plantation. There may thus have been during the 45 or so years since it was clear felled a gradual process of development towards the type of ant community that characterizes Callunetum in this locality. Throughout this period there would have been abundant sources for recolonization in the immediate vicinity for the surrounding land for many square miles was at that time normal heath.

SAMPLING

Early observations showed that the pattern of variation in ant species necessitated a sampling area of several hectares. The 8 ha piece chosen was divided into hectare squares in each of which twenty samples were taken at random (using random numbers and co-ordinates for location). Each sample was obtained by placing a sugar bait (crystalline sucrose in a tin with holes) in the top 5 cm of soil and recording the species of ant on it at weekly intervals. This method of course gave no estimate of the population density, only of the species present.

Sugar baits

At each sample point the height above sea level and three soil factors were measured: moisture (by drying and weighing), organic matter (by combustion) and integrated temperature. In addition the main plants (seven species) and the uncovered soil (in fact surfaced with lichens and mosses) were recorded on a proportionate area basis. Temperature was integrated physico-chemically by placing a unit in the top 5 cm of soil. Each unit consisted of pure glacial acetic acid (about 0·5 ml) in a polythene tube (volume 1 ml) with a pore (diameter 1 mm) through which the acid vapour passed into a sealed outer polythene chamber (about 18 ml volume) containing surplus soda-lime. The structure and proportions of all units were as nearly similar as practicable. They were calibrated at constant temperature (x) and the amount of acid transfused (y) gave the relation $y = a+bx$ (with error variation of course). Over a period (t) the equation became $y = (a+bx)t$ for medium times, though the relation was not applicable for short or long periods. Typical values of b were 4 mg per °C in 4 weeks with coefficient of variation 20%. Of course other fatty acids and other absorbents could be used for other temperature ranges. These units were set in June whilst the soil is still warming up and its temperature very variable and again in August when its temperature is maximal but since the later sampling yielded no meaningful variation comparable with that of June—the area being much more uniformly warm—it has not been included in the analysis.

THE ANTS

The species known to occur in the 8 ha area are:

Formicinae	*Formica cunicularia* Latreille
	F. fusca Linnaeus
	F. transkaucasica Nasonov
	Lasius niger Linnaeus
	L. alienus Forster
	L. flavus Fabricius
Myrmicinae	*Tetramorium caespitum* Latreille
	Anergates atratulus Schenck
	Strongylognathus testaceus Schenck
	Myrmica sabuleti Meinert
	M. ruginodis Nylander
	M. scabrinodis Nylander
Dolichoderinae	*Tapinoma erraticum* Latreille

Altogether, owing to some irregularities in the shape of the area, there were only 157 sample points. After 1, 2, 3, . . . , 8 weeks the numbers occupied by ants were 99, 128, 132, 136, 137, 137, 139, 139. This shows a rapid rate of discovery at first, slowing more and more to a limit which left eighteen (11%) unoccupied. All the species behaved similarly in this respect and there was only one change of occupancy (from *Tetramorim caespitum* to *Formica fusca*). The rate of discovery is in fact well described by a modified exponential equation:

$$y = 137{\cdot}67 - 130{\cdot}94e^{-1{\cdot}2260t} \text{ fitted by least squares}$$

where y = number occupied, and t = time in weeks.

This could be taken to mean that search is random and since it is well known that ants are organized into colonies the random element would relate to worker foraging within

their territories. The 11% of unoccupied stations might arise if the baits fell in suitable but ant-free spaces between colonies or in unsuitable areas or areas which had not yet been colonized.

Of the 139 occupied baits fifty-nine had *Lasius alienus* (42%), thirty-nine *L. niger* (28%), twenty-three *Tetramorium caespitum* (17%), nine *Formica fusca* (6%), three *Myrmica sabuleti*, three *M. scabrinodis*, two *Tapinoma erraticum* and one *Myrmica ruginodis*. Thus 76% were Formicinae, 22% Myrmicinae, and 2% Dolichoderinae: *Lasius* species alone accounted for 70%.

In the further analysis of these results only stations with the four most common species and the ant-free stations can be examined statistically, general observations must suffice for the rest.

THE HABITAT

The correlation coefficients between the twelve variables that characterize the habitat have been calculated and set out in matrix form (Table 1). These are derived from the five group means (four species of ant and no-ants) not from 147 items of station data for the former are theoretically more appropriate in discussing the relations between species.

Table 1. *Correlation matrix (between groups); coefficients* × 100

Variable	Code	1	2	3	4	5	6	7	8	9	10	11	12
Height	1	–	−82	−95	66	99	29	80	−77	−88	−99	24	47
Moisture	2		–	92	−89	−85	−65	−92	99	99	75	−61	−43
Organic	3			–	−81	−96	−39	−82	90	95	93	−51	−58
Temperature	4				–	69	37	88	−90	−87	−63	84	70
Bare	5					–	33	82	−80	−91	−98	26	46
Calluna vulgaris	6						–	52	−68	−60	−15	25	−35
Erica cinerea	7							–	−90	−93	−73	49	40
E. tetralix	8								–	97	70	−67	−42
Molinia caerulea	9									–	83	−55	−44
Agrostis setacea	10										–	−22	−54
Ulex minor	11											–	71
Pteridium aquilinum	12												–

For three degrees of freedom a value of 0·878 has 5% probability and 0·959 has 1% probability.

It should be emphasized that the five sets of group means are not to be interpreted as five random observations from a multivariate distribution. In that case the estimation and further analysis of a correlation matrix based on such a small sample would not be justified. The randomness shows itself in the errors of estimation of the group means, which are themselves fixed quantities. These errors are small compared with between group differences, in view of the reasonable sample size, and they are now being ignored for simplicity. Subsequent analysis is not concerned in any way with statistical inference, but with deriving and interpreting a simple description of the geometrical configuration obtained when the five group means are represented by points in twelve dimensional Euclidean space.

Notice that the correlations with height separate the variables into two clusters: those with positive and those with negative values. Each of these clusters, shows positive correlation between its component variables. The smaller, negative group comprises moisture, organic matter and the plants *Erica tetralix*, L. *Molinia caerulea* (L.) Moench and *Agrostis setacea* Curt. the first two of which at least are well known as inhabitants of wet places which tend to accumulate organic matter. The larger positive and less compact

group comprises height, temperature, bare earth and the plants *Calluna vulgaris*, *Erica cinerea*, L. *Ulex minor* Roth, and *Pteridium aquilinum* (L.) Kuhn. The proportion of uncovered ground is greater on the higher, shallower, better drained and therefore drier soils and this enables the sun to heat the top soil stratum more; all four plants are well-known inhabitants of such dry heath. Of the seven variables in this group, height bare area and the plant *Erica cinerea* show greatest mutual correlation.

Highly intercorrelated sets of data like this can be simplified by compounding the variables into factors or principle components (Kendall 1957; Pearce & Holland 1960). In this case 98% of the dispersion can be accounted for by three components and the coefficients of the twelve variables on these have been tabulated (Table 2).

Table 2. *Principle component coefficients*

Variable	Code	Components I	II	III
Height	1	0·304	−0·001	−0·366
Moisture	2	−0·330	−0·135	−0·111
Organic	3	−0·328	0·040	0·137
Temperature	4	0·306	−0·157	0·286
Bare	5	0·310	0·022	−0·334
Calluna vulgaris	6	0·162	0·631	0·287
Erica cinerea	7	0·311	0·109	0·038
E. tetralix	8	−0·324	−0·139	−0·181
Molinia caerulea	9	−0·334	−0·118	−0·012
Agrostis setacea	10	−0·291	0·098	0·413
Ulex minor	11	0·203	−0·289	0·590
Pteridium aquilinum	12	0·191	−0·647	0·078

The first accounts for 73% of variation and is by far the most important. The two clusters already mentioned, of wet and dry heath, have substantial negative and positive values respectively and it is clear that this component connects a set of variables that are governed by the water content of the soil. As might be expected from its well-known indifference to soil moisture, *Calluna vulgaris* has a small coefficient.

The second accounts for 13% of the dispersion and is not so easy to identify. *C. vulgaris* has, in this case, a large positive value and *Pteridium aquilinum* a large negative value (and *Ulex minor* a moderate negative value) so that the factor whatever it is, separates these two plant species widely. Unfortunately the non-biotic metrics all have small coefficients and provide no clue. However, one possibility is reasonable: plant nutrient status. *Calluna vulgaris* is notable for its ability to live in poor soils whereas *Pteridium aquilinum* and *Ulex* species are well known to be much more dependent on soil nutrients, and in fact, both are used as indicators of good soil in agriculture and forestry. As *Ulex* has root nodules that may fix nitrogen its greater dependence on soil nutrients would be expected. On the whole then a likely identity for the second component is soil nutrient status.

The third component accounts for 12% of the total dispersion. Height and bare ground both have high negative coefficients and temperature quite a large positive one, from which it appears that the factor maintains higher temperatures in low-lying dense vegetation; wind perhaps. The plants *Agrostis setacea* and *Ulex minor* which have strikingly high positive loadings are the two species confined in the British Isles to southern and eastern localities with warm summers and low wind velocities. They are in fact the characteristic associates of *Calluna vulgaris* in lowland heath. The most likely factor here

then, would seem to be wind which cools exposed soil on high ground and is especially strong in the heaths of the north and west.

Hence the three components may be tentatively identified as moisture, nutrient status and wind. By far the greatest part of the variation in heath is caused by the first of these.

ANT DISTRIBUTION

The mean values of the twelve variables for the common species of ant and for unoccupied areas have been tabulated (Tables 3 and 4). Standard errors have been given as an indication of reliability but in such highly correlated data it should be realized that the usual significance tests are inappropriate.

Table 3. *Mean value of height above sea level, three soil factors and the proportion of bare ground for four species of ant and unoccupied areas*

Species	Height (m)	Soil moisture (%)	Soil organic matter (%)	Temperature in June (° C)	Proportion bare (of 8)
Lasius alienus	17·8 ± 0·46	8·8 ± 0·69	17·9 ± 1·06	17·03 ± 0·33	4·04 ± 0·23
Tetramorium caespitum	16·3 ± 0·60	12·5 ± 1·39	22·9 ± 1·82	17·31 ± 0·64	3·05 ± 0·44
No-ants	17·5 ± 0·86	14·1 ± 3·37	21·1 ± 2·34	15·94 ± 0·53	3·84 ± 0·28
Formica fusca	13·6 ± 0·34	21·8 ± 7·28	25·5 ± 4·13	16·76 ± 0·85	1·11 ± 0·48
Lasius niger	14·2 ± 0·60	89·8 ± 15·15	29·7 ± 2·94	15·29 ± 0·39	1·39 ± 0·27

Evidently *Lasius niger* lives in low-lying ground if it is wet, otherwise *Formica fusca* is more likely to be there. Such areas accumulate drifting organic matter especially after fires and decay proceeds slowly. As the soil warms up in spring they lag behind the higher drier areas unless these are exposed to cooling winds or lack insolation through negative aspect or plant shade. About 0·83 of the area is covered by plants (which must also reduce the rate of warming) and about half of this is grass, mainly *Molinia caerulea*; in this respect the habitat is outstanding. *Erica tetralix* and *E. ciliaris* L. are more common than *Calluna vulgaris*, and *Erica cinerea* is absent; *Ulex minor* and *Pteridium aquilinum* are sparse. The ants *Myrmica scabrinodis* and *M. ruginodis* occur with *Lasius niger*, but infrequently.

Table 4. *Proportion (out of 8) of the main plants associated with four ant species and unoccupied areas*

Species of ant	*Calluna vulgaris*	*Erica cinerea*	*E. tetralix*	*Molinia caerulea*	*Agrostis setacea*	*Ulex minor*	*Pteridium aquilinum*	Others
Lasius alienus	0·78 ± 0·15	0·51 ± 0·11	< 0·05	0·10 ± 0·09	0·14 ± 0·09	1·04 ± 0·19	0·70 ± 0·22	0·77
Tetramorium caespitum	0·92 ± 0·35	0·69 ± 0·22	< 0·05	0·31 ± 0·21	0·44 ± 0·23	1·04 ± 0·30	0·57 ± 0·25	0·93
No-ants	1·28 ± 0·33	0·50 ± 0·22	0·11 ± 0·15	0·22 ± 0·19	0·28 ± 0·32	0·45 ± 0·25	0·22 ± 0·21	1·10
Formica fusca	1·34 ± 0·70	0·22 ± 0·79	< 0·05	0·89 ± 0·84	0·89 ± 0·47	1·45 ± 0·65	0·44 ± 0·29	1·66
Lasius niger	0·52 ± 0·21	0·03 ± 0·09	1·29 ± 0·21	2·23 ± 0·28	0·69 ± 0·26	0·57 ± 0·19	0·44 ± 0·24	0·84

Formica fusca though living low down is found in drier and warmer areas than *Lasius niger* but with a substantial amount of organic matter, perhaps in this case alive, for the vegetation cover (0·85) is greater than elsewhere. The grasses comprise about a third of this but *Agrostis setacea* is as common as *Molinia caerulea*. Most outstanding is the high proportion of *Calluna vulgaris* and *Ulex minor* each of which accounts for about a quarter of the vegetation. This habitat is richer than the others in infrequent plants that have not been specified.

The *Tetramorium caespitum* habitat differs much less from that of *Formica fusca* than the *F. fusca* does from *Lasius niger*. It is a little higher up than *Formica fusca* in rather drier and perhaps a slightly warmer area. But the main difference is in the extent of the vegetation cover which only amounts to 0·62. Also the grasses are still less frequent (0·15 of vegetation), though again about equally represented. Most characteristic perhaps is the fact that *Erica cinerea* is at its maximum and nearly as common as *Calluna vulgaris* (whereas *Erica tetralix* is absent). *Ulex minor* though slightly less frequent than in *Formica fusca* areas is the single best represented plant species.

Lasius alienus lives in rather drier and less organic soil than *Tetramorium caespitum* but hardly any higher and no warmer. There is even less vegetation—about half is bare soil—and the grasses are almost absent but the proportions of the other main plants are much the same.

FIG. 1. The proportions bare and variously vegetated in the areas inhabited by ants and not. (a) No ants; (b) *Lasius alienus*; (c) *Tetramorium caespitum*; (d) *Lasius niger*; (e) *Formica fusca*.

Ant-free areas are quite high in the *T. caespitum–Lasius alienus* zone, but are almost as cold as the wet bog in June. They are moister than the *L. alienus* areas but resemble them in that about half the ground is bare. In the vegetation *Calluna vulgaris* predominates (about 0·5) and it is as common as in *Formica fusca* areas. Also outstanding is the scarcity of *Ulex minor*, less than in any other area and notably less than in the *Lasius alienus* habitat which this region resembles most in other respects: in fact it is almost true to say that the ant-free areas are *Lasius alienus* habitat in which *Ulex minor* is largely replaced by *Calluna vulgaris* and the two grasses. These unoccupied areas then are not spaces between nests and probably not places yet to be colonized, but are unsuitable on account of their cool micro-climate and lack of *Ulex minor* (an important legume which carries a rich aphid population and harbours many other insects).

Myrmica sabuleti, represented at three stations close together, lives in a slightly drier soil than *Formica fusca* with about a quarter of the soil exposed. The two grasses *Molinia caerulea* and *Agrostis setacea* (in proportion 1 : 2) are the main plants. The abundance of *A. setacea* is the outstanding feature.

Table 5. *Ant species ranking for all twelve variables: the ranks of variables* 2, 3, 8, 9, 10 *have been reversed*

Group	Variables and code numbers												Sum	Mean
	1 Height	2 Moisture	3 Organic	4 Temperature	5 Bare	6 *Calluna vulgaris*	7 *Erica cinerea*	8 *E. tetralix*	9 *Molinia caerulea*	10 *Agrostis setacea*	11 *Ulex minor*	12 *Pteridium aquilinum*		
Lasius alienus	1	1	1	2	1	4	2	2	1	1	2	1	19	1·6
Tetramorium caespitum	3	2	3	1	3	3	1	3	3	3	3	2	30	2·5
No-ants	2	3	2	4	2	2	3	4	2	2	5	5	36	3·0
Formica fusca	5	4	4	3	5	1	4	1	4	5	1	3	40	3·3
Lasius niger	4	5	5	5	4	5	5	5	5	4	4	4	55	4·6

Ranking

The rank of the five groups can be considered for each of the twelve variables and the degree of agreement or concordance measured (Table 5). (Ranking must be reversed for the set of five variables that correlate negatively with height and give negative coefficients for the first principle component.) *Lasius alienus* comes first in seven and second in four cases and only ranks lower in the *Calluna vulgaris* sequence. *Lasius niger* by contrast ranks last in seven and fourth in five cases. If the ranks are summed the sequence: *L. alienus*, *Tetramorium caespitum*, no-ants, *Formica fusca* and *Lasius niger* is obtained and the coefficient of concordance (W) has the value 0·51 ($P<0·001$) so that there is considerable 'agreement' between variable rankings (Moroney 1956).

Principle components

Each species of ant and no-ants has a position in the model space defined by the three components. The species value for each of these is calculated by summing the products of the means and the appropriate standardized coefficients.

Table 6. *Species loadings on the first three principle components and their distances apart in the three dimensional space*

Species	Component I	II	III	Distances: *Lasius alienus*	*Tetramorium caespitum*	No-ants	*Formica fusca*
L. alienus	13·19	−5·03	4·61	–			
T. caespitum	12·41	−4·09	5·90	1·77	–		
No-ants	11·88	−1·08	3·62	4·28	3·81	–	
F. fusca	10·18	−3·03	8·73	5·48	3·76	5·73	–
L. niger	6·91	−4·75	4·28	6·29	5·77	5·85	5·78
Mean	10·91	−3·60	5·43				

In relation to the first component the species values should form a sequence similar to the over-all rank (Kendall 1957). This is indeed the case (Table 6): *L. alienus*, *Tetramorium caespitum* and no-ants form a close association at intervals of less than 1 unit; *Formica fusca* stands 1·7 units from the nearest (no-ants) and *Lasius niger*, 5 units, the distance between them being 3·3 (see Fig. 2). Thus the wetness of the *L. niger* habitat is represented in this model by its separation from the other ants in relation to the first (water) component.

The second component produces a totally different arrangement. 'No-ants' stands 2 units away from the nearest (*Formica fusca*). This is about 1 unit from *Tetramorium caespitum* which is less than 1 unit from the extremely close *Lasius* species. The implication is that ants do not occur in areas poor in plant nutrients (it will be recalled that half the area is bare and half the vegetation is *Calluna vulgaris* whilst *Ulex minor* is unusually infrequent), but that the two *Lasius* species though highly dissimilar in relation to water supply both live in nutrient-rich ecosystems.

The third shows *Formica fusca* well above average and the two *Lasius* species (again together) and 'no-ants' below average. If this component represents wind exposure it is not surprising to find *Formica fusca* which is the only completely above-ground hunter, living in sheltered places. The position of *Lasius niger* close to *L. alienus* may be taken to indicate that it is low living because of the moisture and its associated vegetation rather than the shelter (it tends Coccidae on *Molinia caerulea*).

The distances apart of the species groups in this model can be calculated (Table 6); they represent their degree of distributional dissimilarity. *Lasius alienus* and *Tetramorium caespitum* are close together (less than half the distance between *T. caespitum* and *Formica fusca* the next nearest), but the rest for various reasons are well spaced out. It is perhaps not over-simplifying to say that *Lasius niger* is separated from the others by component 1 (water), 'no-ants' by component 2 (nutrient supply) and *Formica fusca* by component 3 (wind exposure). The remaining two, *Lasius alienus* and *Tetramorium caespitum*, co-exist in most areas of dry heath though as already mentioned there is a tendency for the former to be relatively more common in higher, drier, more mineral soils with sparser vegetation comprising fewer grasses.

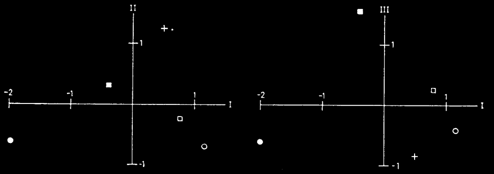

FIG. 2. Species positions in the component space; deviations from mean at origin. ○, *Lasius alienus*; ●, *L. niger*; ■, *Formica fusca*; □, *Tetramorium caespitum*; +, no-ants.

DISCUSSION

Since the species of ant are not randomly distributed but have acquired some relation to the pattern of habitat variation it must be presumed that mechanisms of assortment exist. There are of course two obvious ones: first, that the queens have some power to select the best habitat in which to live, and although quite clearly there must be a strong bias in favour of those able to do this, the difficulties of developing a guidance system that responds appropriately must be considerable. Second, the colonies once established may further assort themselves through population pressure largely dependent on the success with which they exploit their immediate resources and their potentiality for aggression. It is hoped to throw light on these processes in later papers.

Ecological distribution

Differences in the habitats occupied by *Lasius niger* and *L. alienus* are frequently reported and it is generally agreed that in north and central Europe *L. alienus* is restricted to dry open places whereas *L. niger* ranges widely (Gösswald 1932, 1951; Šilhavý 1938; Wilson 1955; Collingwood 1957). Elsewhere, however, this does not seem to be the case; in the Mediterranean area both may be found thought not necessarily together, in gardens, scrub and woodland and *L. alienus* forages epigaeically (Bernard 1956; Collingwood 1956), similarly in Hokkaido, Japan (Hayashida 1960). In North America, *L. alienus* is usually found in woodland except at high altitudes when it may appear in the open (Wilson 1955) and Wilson's suggestion that this is due to competitive exclusion by *L. niger* in Europe and by *L. neoniger* in America both of which are conspicuously eurytopic, is interesting.

Diver (1938, 1940) working near the locality of the present study found that whereas *L. niger* was widespread and lived in sand dunes, wet and dry heath, marsh, grassland, scrub and woodland, *L. alienus* was almost restricted to dry heath. Furthermore it appeared to predominate in heath formed on blown sand rather than the older consolidated eocene (Bagshot) sands which were often occupied by *L. niger* as were the damp hollows between ridges. Although in the part of Hartland Moor studied intensively *L. niger* was restricted to wet heath it is a matter of common observation that it is eurytopic and occurs in scrub and gardens and especially roadside verges. It also occurs in pasture provided stones are available as nest sites (for unlike *L. flavus* this species is unable to build mounds strong enough to resist heavy grazing animals). The essential factor common to all these situations is unknown but it might be low wind, high humidity or moderate warmth or something of all three; the food supply is as variable as the vegetation.

T cae. *Tetramorium caespitum* is known as the turf-ant in Germany where it is distinctly eurytopic (Gösswald 1932, 1951). It is well represented in steppe in Moravia (Šilhavý 1938). In Italy it may occur in city pavements and a variety of other habitats. In Hokkaido Hayashida (1960) found it in scrub or woodland and rarely in very dry and exposed situations. Whilst it is most common in Callunetum in this country it does occur occasionally in turf in warm sunny places. There seems to be no doubt that the variety of habitat occupied is much reduced towards the north of the geographical range.

Geographical distribution

As already implied these species are widely distributed in Eurasia and occur in America. Their northerly extension in Britain is interesting as it corresponds with the temperature relation found in this study. According to Collingwood (1957, 1961) *Lasius niger* 'is common in sheltered river valleys as far north as the Oykell in Sutherland'; *Formica fusca* is 'local to the north of the English Midlands and has only been found in Scotland in a few localities in the west'; *Lasius alienus* 'occurs sporadically as far north as south-west Scotland but is characteristic of dry heaths and uplands in south Britain'; whilst the distribution of *Tetramorium caespitum* 'north of the heathlands of south England is almost entirely coastal and is very scattered in Scotland'. This broadly indicates that *Lasius niger* ranges all the way, *Formica fusca* half way and the other two only a small part of the way from the south coast northwards. The tendency to occur on the west coast is interesting because the hours of sunshine in May and June are as high on the coasts round the Irish Sea as they are in the south of England, which presumably means that the soil surface temperatures can be raised and the ants can find suitable nesting places. The line joining points having 6½ h sunlight in June fits the British limits of *Lasius alienus* quite well. *Tapinoma erraticum* is well fitted by the 7 h line.

L. niger F. fusca L. al T. cas Tap

The ant fauna of upland heath occurring in the north and west of Britain is quite different (Brian & Brian 1951; Brian 1952, 1955, 1956a, b; Collingwood 1961). Transitions from one to the other may be seen on Black Down in west Dorset and Bovey Heath just east of Dartmoor.

ACKNOWLEDGMENTS

I wish to thank Mr P. Holgate for much advice on statistical treatment of the data and for arranging computer analyses; also many other colleagues for invaluable help.

SUMMARY

The heath was sampled for ants, height above sea level, soil moisture and organic matter, soil temperature and vegetation cover.

The particular features of the habitat of each species of ant and of the ant-free areas are described. The variables measured were highly correlated and the data was further analysed by principle component methods.

Various influences emerged, notably that ants are absent from areas that can probably be characterized as relatively infertile and that, though dry, are cool in early summer; that two species of *Lasius* differ in relation to water supply; and that the unrelated *L. alienus* and *Tetramorium caespitum* co-exist in dry heath with only a tendency to differential environmental frequencies.

REFERENCES

Bernard, F. (1956). Remarques sur le peuplement des Baléares en Fourmis. *Bull. Soc. Hist. Nat. Afr. N.* 47, 254–66.

Brian, M. V. (1952). The structure of a dense natural ant population. *J. Anim. Ecol.* 21, 12–24.

Brian, M. V. (1955). Food collection by a Scottish ant community. *J. Anim. Ecol.* 24, 336–51.

Brian, M. V. (1956a). The natural density of *Myrmica rubra* and associated ants in west Scotland. *Insectes Sociaux*, 3, 473–87.

Brian, M. V. (1956b). Segregation of species of the ant genus *Myrmica*. *J. Anim. Ecol.* 25, 319–37.

Brian, M. V. & Brian, A. D. (1951). Insolation and ant population in the west of Scotland. *Trans. R. Ent. Soc. Lond.* 102, 303–30.

Collingwood, C. A. (1956). Ant hunting in France. *Entomologist*, 89, 105–8.

Collingwood, C. A. (1957). The species of ants of the genus *Lasius* in Britain. *J. Soc. Brit. Ent.* 5, 204–14.

Collingwood, C. A. (1961.) Ants in the Scottish Highlands. *Scot. Nat.* 70, 12–21.

Diver, C. (1938). The plant-carpet in relation to animal distribution. *Proc. Linn. Soc. Lond.* 150 (3), 124–35.

Diver, C. (1940). The problem of closely related species living in the same area. In J. S. Huxley, *The New Systematics*, pp. 303–28. Oxford.

Diver, C. & Diver, P. (1933). Contributions towards a survey of the plants and animals of South Haven Peninsula, Studland Heath, Dorset. 3. Orthoptera. *J. Anim. Ecol.* 2, 36–69.

Diver, C. & Good, R. D'O. (1934). The South Haven Peninsula survey (Studland Heath, Dorset): general scheme of the survey. *J. Anim. Ecol.* 3, 129–32.

Good, R. D'O. (1935). Contributions towards a survey of the plants and animals of South Haven Peninsula, Studland Heath, Dorset. 2. General ecology of the flowering plants and ferns. *J. Ecol.* 23, 361–405.

Good, R. D'O. (1948). *A Geographical Handbook of the Dorset Flora.* Dorset Natural History and Archaeological Society.

Gösswald, K. (1932). Ökologische Studien über die Ameisenfauna des mittleren Maingebietes. *Z. wiss. Zool.* 142, 1–156.

Gösswald, K. (1951). Zur Ameisenfauna des Mittleren Maingebietes mit Bemerkungen über Veränderungen seit 25 Jahren. *Zool. Jb. (Syst.)*, 80, 507–32.

Hayashida, K. (1960). Studies on the ecological distribution of ants in Sapporo and its vicinity (1 et 2). *Insectes Sociaux*, 7, 125–62.

Kendall, M. G. (1957). *A Course in Multivariate Analysis*. London.

Lack, D. & Venables, L. S. V. (1937). The heathland birds of South Haven Peninsula, Studland Heath, Dorset. *J. Anim. Ecol.* 6, 62–72.

Moroney, M. J. (1956). *Facts from Figures*. London.

Pearce, S. C. & Holland, D. A. (1960). Some applications of multivariate methods in Botany. *Appl. Stat.* 9, 1–7.

Šilhavý, V. (1938). Mravenci hadcové stepi u Mohelna. Sborník Přírodovědeckého Klubu v Třebíči. *Ročnik*, 2, 24.

Tansley, A. G. (1939). *The British Islands and their Vegetation*. Cambridge.

Wilson, E. O. (1955). A monographic revision of the ant genus *Lasius*. *Bull. Mus. Comp. Zool. Harvard*, 113 (1), 1–199.